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Soil Biology & Biochemistry 34 (2002) 263–271

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Microbial activity and nitrogen mineralization in forest mineral soils following heating: evaluation of post-fire effects

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Received 5 September 2000; received in revised form 12 April 2001; accepted 12 September 2001

Abstract

Heat generated during fire induces chemical oxidation of soil organic matter thereby altering carbon (C) and nitrogen (N) transformations. Prior soil fire history and soil moisture content at the time of heating can be confounding factors in the interpretation of the influence of heat on soil processes. In this study we evaluated how soil heating (160 and 380°C) under three moisture regimes (−0.03, −1.0, and −1.5 MPa) influences microbial activity and N mineralization in two soils: (1) not exposed to fire for the past 80 years, (2) recently exposed to wildfire. Initially, the fire exposed soil had lower basal respiration rates and lower concentrations of microbial biomass C, potentially mineralizable nitrogen (PMN), soluble hexose sugars, and NH_4^+–N, but higher NO_3^-–N concentrations than the soil not exposed to fire. Both soils responded similarly to elevated temperatures. Higher temperatures resulted in greater microbial mortality and a greater release of soluble sugars and NH_4^+–N. PMN concentrations increased at 160°C, but decreased at 380°C in both soils. The highest NH_4^+–N concentrations were observed in soils not previously exposed to fire that were incubated at −0.03 MPa after heating. Soils previously exposed to fire had low NH_4^+–N concentrations and high NO_3^-–N concentrations. Heating at low soil water potentials resulted in elevated concentrations of microbial biomass C and soluble sugars, and lower NH_4^+–N and NO_3^-–N concentrations. Initial C availability appeared to be an important factor in the recovery of microbial biomass during 14-d post-heating incubation, which was greatest after heating at 380°C and −1.5 MPa. Both soils demonstrated slow rates of recovery of nitrifying organisms despite high rates of net NH_4^+–N accumulation. It appears that low soil water potential at the time of heat exposure reduces losses of mineralizable N.

Keywords: Nitrification; Labile N; Available C; Forest soils

1. Introduction

The effect of fire induced soil heating on carbon (C) and nitrogen (N) dynamics in forest mineral soils has received only limited scientific attention. It is known that fire enhances chemical oxidation of soil organic matter thus altering its chemical composition (Fernandez et al., 1997), but the degree of organic matter oxidation depends on temperatures generated by fire, fire duration, and heat penetration (Hungerford et al., 1991). Temperatures higher than 50°C result in death of heat-sensitive microbes (fungi more so than bacteria) and temperatures higher than 70°C can directly affect vegetation (Hernandez et al., 1997; Neary et al., 1999). Subsequently, dead plant and microbial biomass can be rapidly oxidized contributing to the pulse of inorganic N that typically follow burning (Diaz-Ravina et al., 1996). However, the combustion of organic matter at exceedingly high temperatures can result in volatilization and potential loss of N previously found in complex organic forms (Giovannini et al., 1990).

Soil moisture content may become a confounding factor in assessing the impact of fire on soil biological and chemical properties (Albini and Reinhardt, 1995). Increased soil temperatures cause the mineral soil and soil water to conduct heat as two independent media depending on their respective specific heat and heat conductivity characteristics (Campbell et al., 1994; Hungerford et al., 1991). Although heat in moist soil is transported faster and penetrates deeper at temperatures below 95°C, latent heat of vaporization prevents soil temperatures from exceeding 95°C until water completely vaporizes. This latent heat effect would not protect heat-sensitive microbes (described earlier) and once water is vaporized, it would be lethal to most heat tolerant microbes (Baker, 1970).

Prescribed burning is often implemented for improving stand quality and soil nutrient concentrations in ecosystems that have been fire-excluded for a significant amount of time (Arno et al., 1995). In order to avoid the risk of wildfire,

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0038-0717/02/$ - see front matter
PII: S0038-0717(01)00180-8

Table 1
Selected soil chemical and physical characteristics: total C, total N, microbial biomass C, and PMN for two soils either not exposed to fire for 80 years or recently exposed to wildfire

Soil	pH	Sand (%)	Clay (%)	Total C (g kg^{-1})	Total N (g kg^{-1})	Biomass C (μg g^{-1})	PMN (μg g^{-1})
No prior fire	5.5	27	10	32	1.3	129	16.2
Fire exposed	6.0	25	11	51	2.6	108	0.2

prescribed fire is frequently performed during moist seasons such as late winter and spring (Dunn et al., 1985). In contrast, most spontaneous wildfires typically occur during dry seasons, summer and fall, when soil water and organic layer moisture are depleted.

A better understanding of the effect of moisture, fire intensity, and fire history on post-burn soil ecosystem recovery could provide a basis for improved prescriptions that better enable restoration of fire dependent forests. The purpose of the work reported was to study changes in microbial activity and N mineralization as affected by soil moisture and temperature regimes to simulate the impact of low and medium intensity fires on the mineral soil surface during wet and dry seasons and compare that impact in soils of different fire history.

2. Materials and methods

2.1. Soil characteristics

Soils were collected from a ponderosa pine (*Pinus ponderosa* Laws.)/Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forest in western Montana. One set of soils was collected from a site that had not been exposed to fire for the last 80 years and the second set of soils was collected from a neighboring site (same soil map unit and same site history) that had been exposed to a high severity wildfire in August 1996 (see Choromanska and DeLuca, 2001). These sites were located on an NE aspect of 35–40% slope, at 1520 m elevation. The mean annual temperature was 7°C with annual precipitation of 44 cm. Soils were loamy-skeletal, mixed, frigid Lithic Ustochrepts formed on granite residuum. Selected soil characteristics are provided in Table 1. Soils were collected from each site in September 1996. In samples of mineral soil (0–10 cm), mixed and all visible debris and coarse fragments were removed. Soils were sieved (2 mm sieve), air-dried, and stored for 9 months prior to use.

In June 1997, four subsamples were drawn from the bulk soils individually, and water content at −0.03, −1.0 and −1.5 MPa was determined using pressure plate and pressure membrane apparatus as described by Klute (1986). Subsequently, soils were split into three equal parts, moistened to −0.03, −1.0, and −1.5 MPa water potential, and then pre-incubated for 14-d at 25°C with moisture monitored and corrected daily based on change in mass. At the end of the pre-incubation period, 60 g subsamples of soil were transferred to sealed metal canisters (six replicate canisters per treatment) and placed in a preheated muffle furnace for 30 min at 25 (control), 160 or 380°C to simulate surface temperatures associated with low and medium intensity fires (Chandler et al., 1983). The limited heat transfer into mineral soil during fire events precludes the direct extrapolation of these results to natural soils below a depth of approximately 3 cm with the exception of heating under large woody fuels and during the burning of pled forest harvest residuals. Soils were allowed to cool and three replicate canisters per treatment were immediately processed and analyzed while the remaining three had their complete contents transferred to 1 l glass jars. These samples were then inoculated with 1 g of unheated soil and the moisture content returned to 0.3, 1.0, or 1.5 MPa water potential. The jars were then sealed and placed in a constant temperature chamber (Fisher Isotemp, Fisher Scientific, Pittsburgh, PA) and incubated for 14-d at 25°C with moisture content checked and corrected daily based on change in mass.

2.2. Laboratory analyses

Soil samples were both extracted immediately after heating (unheated control soils included) and 14-d post-heat treatment. Fresh, 25 g oven-dry equivalent, soil samples were shaken with 50 ml of 2 M KCl for 30 min and filtered through Whatman #42 filter paper. Extracts were analyzed for NH_4^+–N using the Berthelot reaction (Willis et al., 1993) and NO_3^-–N by nitration of salicylate (Yang et al., 1998). Microbial biomass was determined by fumigation/extraction and reaction with ninhydrin as described by Joergensen and Brookes (1990) and modified by DeLuca and Keeney (1993). Microbial biomass C was calculated as difference between ninhydrin-reactive N in fumigated samples and non-fumigated samples multiplied by a factor of 21 (Joergensen and Brookes, 1990).

Potentially mineralizable nitrogen (PMN) was determined by a 14-d anaerobic incubation in which 5 g of moist soil and duff was placed in a centrifuge tube with 12.5 ml of distilled-deionized water and the head space was displaced by N_2 gas (Hart et al., 1994). After a 14-d incubation at 25°C, 12.5 ml of 4 M KCl was added to each tube, the tubes placed in a shaker for 30 min. Soil extracts were then filtered and analyzed for NH_4^+–N, as described above. Values for PMN reflect the difference between the incubated samples and the non-incubated NH_4^+–N value.

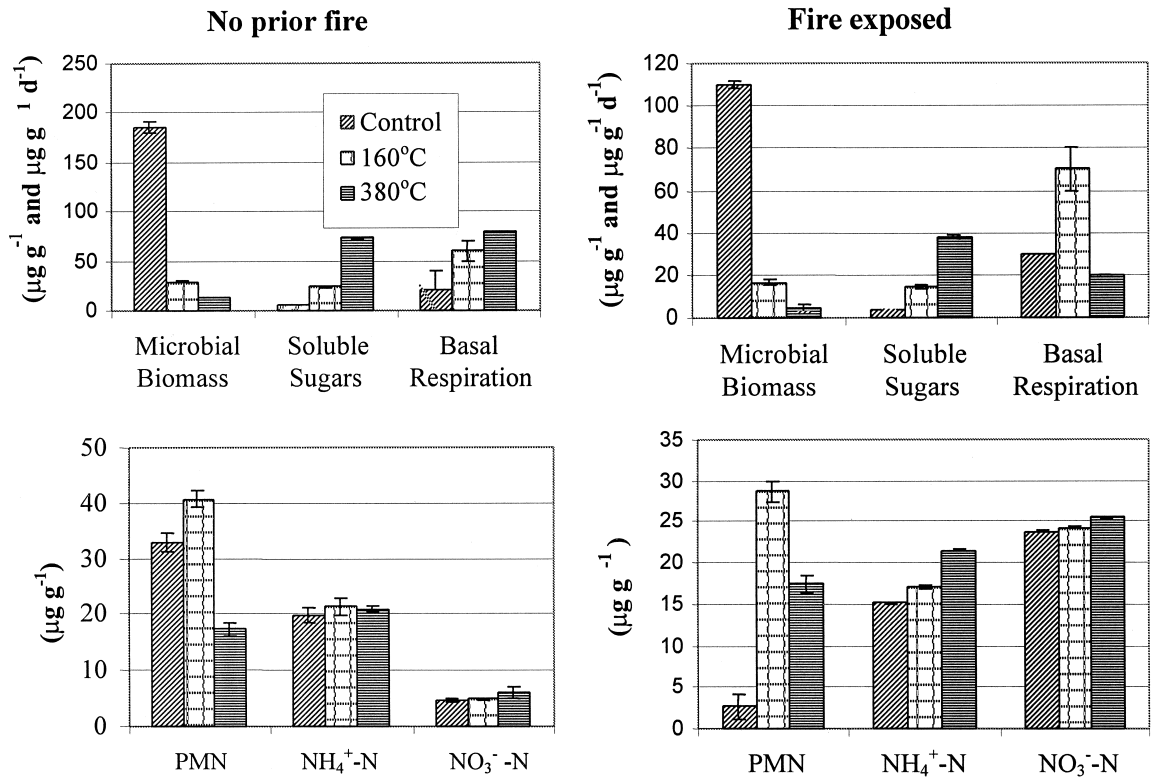

Fig. 1. Soil microbial biomass C, soluble hexose sugars (ARC), basal respiration, PMN, NH_4^+–N, and NO_3^-–N measured immediately after exposure to three different temperatures (25, 160, or 380° C) and averaged across three moisture levels (error bars indicate ±1SE).

Soluble hexose sugar concentrations measured as anthrone reactive carbon (ARC) were determined on 0.5 M K_2SO_4 extracts obtained from 25 g of fresh soil (soil to extract ratio of 1:2) and analyzed within 48 h as described by DeLuca (1998). Microbial respiration was measured during 3-d aerobic incubation by using alkaline traps (Zibilske, 1994). Fresh 50 g soil samples were brought to 60% water holding capacity and placed in 1 l glass jars. An open scintillation vial containing 20 ml of 1N NaOH was carefully snugged into the soil, then the jar was sealed and incubated at 25°C for 3-, 7- and 14-d. The contents of these vials were then quantitatively transferred to 200 ml conical flasks, and 24 ml of 2N $BaCl_2$ and five drops of phenylthaleine indicator solution were added, and the solution titrated with 1.0N HCl to a clear end point.

2.3. Statistical analysis

The experiment sample was incubated in a completely randomized, $2 \times 3 \times 3$ factorial arrangement representing two soils, three temperatures and three soil moisture contents, with each treatment replicated three times. All data were found not to violate assumptions of ANOVA. Data were then analyzed by using a three-way ANOVA. All data were analyzed using Statistical Analysis System (SAS Institute, 1995).

3. Results

3.1. Immediate treatment effects

Soil biochemical response to heating was greatly influenced by recent fire history. Soils with recent exposure to wildfire initially had higher concentrations of total C, N and lower microbial biomass C and PMN (Table 1).

Microbial biomass C declined immediately after heating with the most severe decline being observed at 380°C (Fig. 1). However, there was a significant interaction between soil fire history and heating temperature for microbial biomass C across all moisture levels (Table 2). Soils not previously exposed to fire had greater microbial biomass C concentration than the fire exposed soils when heated at 160 or 380°C. Although both soils demonstrated a similar reduction in biomass C at 160°C compared to the respective unheated control soil, temperature increase to 380°C resulted in a greater reduction biomass C in the fire exposed soil than in the soil not previously exposed to fire (Fig. 1). Soil history, temperature and soil water potential had no significant effect on basal respiration rates immediately after heating.

Concentrations of soluble sugars were significantly increased immediately following heating (Table 2). Concentrations of soluble sugars increased by a factor of 4 at 160°C and almost a factor of 12 at 380°C (Fig. 1). Heating at 380°C had a greater effect on the release of

Table 2
ANOVA for microbial biomass C, soluble sugars and basal respiration (CO_2 evolution) for two soils (no prior fire and fire exposed soil) immediately after exposure of soil to three temperatures at three soil water potentials

	Source	d.f.	MS	*F* value	*P* > *F*
Biomass C	Soil	1	13,867	26.8	0.0001
	Temperature	2	1,05,559	203.8	0.0001
	Soil × Temperature	2	6508	12.6	0.0005
	Moisture	2	2656	5.1	0.0190
	Soil × Moisture	2	2073	4.0	0.0389
	Error	16	518		
Soluble ARC	Soil	1	3444	66.7	0.0001
	Temperature	2	12,323	26.7	0.0001
	Soil × Temperature	2	1377	23.2	0.0001
	Moisture	2	593	11.5	0.0008
	Soil × Moisture	2	36	0.7	0.5156
	Error	16	52		
CO_2 evol.	Soil	1	0.102	1.9	0.3045
	Temperature	2	0.028	0.5	0.6642
	Soil × Temperature	2	0.084	4.0	0.3926
	Moisture	2	0.220	7.7	0.1985
	Soil × Moisture	2	0.420	3.9	0.1146
	Error	16	0.098		

soluble sugars from the soil not exposed to fire compared to the previous fire exposed soil.

Both soils heated at 160°C had, on average, twice the PMN concentrations as the unheated control, while at 380°C PMN declined to levels comparable to those in the control soils (Fig. 1). Despite similar PMN levels at 380°C, the overall labile N concentrations declined in the soil not exposed to fire to 50% that of the initial control levels, but increased by a factor of six times in the fire exposed soil (Fig. 1). Soil heating resulted in NH_4^+–N release from the oxidized organic matter and, on average, there was a 10% concentration increase at 160°C and a 22% increase at 380°C compared to the unheated control (Table 3 and Fig. 1). In contrast, increased temperatures had no significant effect on NO_3^-–N concentrations in both soils despite their different fire history (Table 3).

Table 3
ANOVA for PMN, extractable soil NH_4^+–N and NO_3^-–N for two soils (no prior fire and fire exposed soil) immediately after exposure of soil to three temperatures at three soil water potentials

	Source	d.f.	MS	*F* value	*P* > *F*
PMN	Soil	1	2668	58.5	0.0001
	Temperature	2	1765	38.7	0.0001
	Soil × Temperature	2	1059	23.2	0.0001
	Moisture	2	167	3.7	0.0485
	Soil × Moisture	2	128	2.8	0.0902
	Error	16	46		
NH_4^+–N	Soil	1	110	24.9	0.0001
	Temperature	2	65	14.7	0.0002
	Soil × Temperature	2	39	8.8	0.0026
	Moisture	2	618	139.4	0.0001
	Soil × Moisture	2	729	164.6	0.0001
	Error	16	4.4		
NO_3^-–N	Soil	1	4984	1240.8	0.0001
	Temperature	2	11.5	2.9	0.0867
	Soil × Temperature	2	0.168	0.04	0.9590
	Moisture	2	385.8	96.1	0.0001
	Soil × Moisture	2	515.2	128.3	0.0001
	Error	16	4		

The effect of water potential and the interaction between water potential and soil history significantly influenced microbial activity and N transformations when averaged across all temperatures (Tables 2 and 3). Lower soil water potential resulted in higher concentrations of microbial biomass C, soluble sugars, and PMN in both soils.

There was also a significant interaction between soil fire history and heating temperature for NH_4^+–N when averaged across moisture levels (Table 3). Although both soils demonstrated a moderate increase (9–13%) in NH_4^+–N concentration when heated at 160°C, heating at 380°C caused a 42% increase in NH_4^+–N concentration in the fire exposed soil and only a 6% increase in the soil not exposed to fire when compared to unheated controls.

The interaction between soil history and water potential also played an important role in N mineralization (Table 3). Soil not previously exposed to fire had a much higher NH_4^+–N concentrations when incubated at a water potential of −0.03 MPa compared to −1.0 and −1.5 MPa where soils exposed to fire had no differences in NH_4^+–N levels with increasing soil water potential in, but significantly higher NO_3^-–N concentrations at low water potentials (Fig. 2).

3.2. Treatment effects 14-d after heating

Microbial activity and C and N mineralization during the 14-d incubation were significantly influenced by soil fire

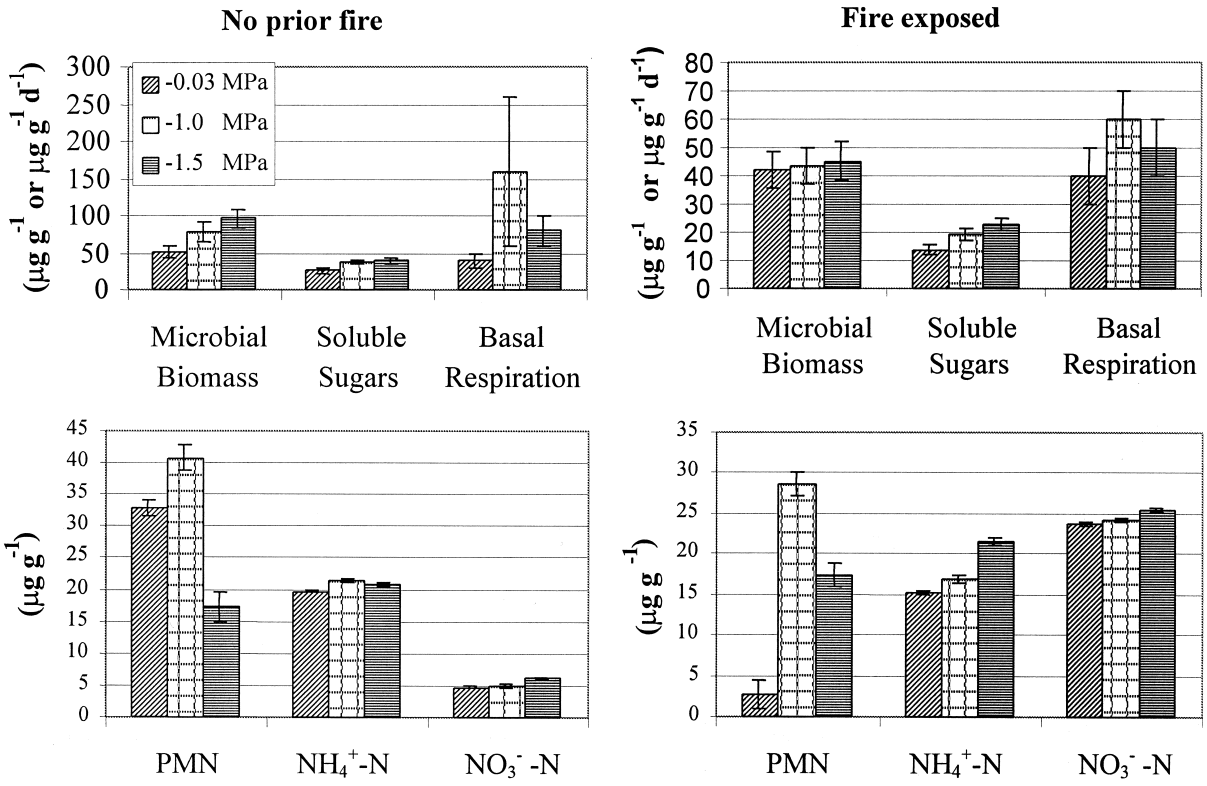

Fig. 2. Soil microbial biomass C, soluble sugars, basal respiration, PMN, NH_4^+–N, and NO_3^-–N at 0.03, 1.0, and 1.5 MPa water potential measured immediately after exposure to heat treatments and averaged across three temperatures (error bars indicate ±1SE).

history, initial heat treatment, and soil water potential (Figs. 3 and 4). Soil microbial biomass C was greatest in both soils when heated to 380°C at −1.5 MPa while the lowest microbial biomass C concentrations were observed when soils were heated at 380°C at −0.03 MPa water potential (Fig. 3).

There was a significant drop in the soluble sugars in both soils with time, however, these concentrations remained elevated when compared to the unheated control (Fig. 3). Heating to 380°C resulted in the highest soluble sugar concentrations 14-d following treatment in both soils. A negative correlation between soil water potential and soluble sugars was observed for both soils in which drier soils had greater levels of soluble sugar accumulation.

Cumulative CO_2 evolution was generally greatest at −0.03 MPa in both soils with the exception of the unheated control of the soil not exposed to fire which had the highest microbial biomass C and soluble sugar concentrations (Fig. 3). The lowest CO_2 evolution was observed in the soils previously exposed to fire and incubated at −1.5 MPa.

PMN also changed over the 14-d incubation period in the two soils, and while it remained consistently higher in the soils not previously exposed to fire, there was a markedly lower PMN content in soils treated with heat at high water potential (Fig. 4). Ammonium–nitrogen concentrations in the unheated soils that were previously exposed to fire soils dropped below the levels recorded prior to incubation, followed by increase in NO_3^-–N concentration (Fig. 4).

4. Discussion

4.1. Immediate treatment effects

Low initial concentrations of microbial biomass C observed in the soils previously exposed to fire likely resulted from C substrate loss during fire and to fire-induced microbial mortality (Choromanska and DeLuca, 2001). Concurrently, reduced levels of NH_4^+–N and PMN in combination with significantly greater NO_3^-–N levels suggest enhanced nitrification in the same soil. In contrast the low NO_3^-–N concentrations in soils not previously exposed to fire may be a result of low initial populations of nitrifiers from conditions brought about by fire exclusion (Neary et al., 1999).

The large decline in microbial biomass C following heating observed here is similar to the range of decline reported by Hernandez et al. (1997) and Prieto-Fernandez et al. (1993). Neary et al. (1999) suggested that most living organisms are killed at temperatures between 50 and 120°C and that fungi are more heat-sensitive than bacteria. Microbial mortality was greatest in the moist soils likely as a result of more effective latent heat penetration and faster heat dissemination than in drier soils (Hartford and Frandsen, 1992; Campbell et al., 1994). Consistently moist soil conditions prior to heating may increase microbial susceptibility to heat effects (Dunn et al., 1985). In contrast, higher rates of survival in dry soils may have been, in part, a result of spore

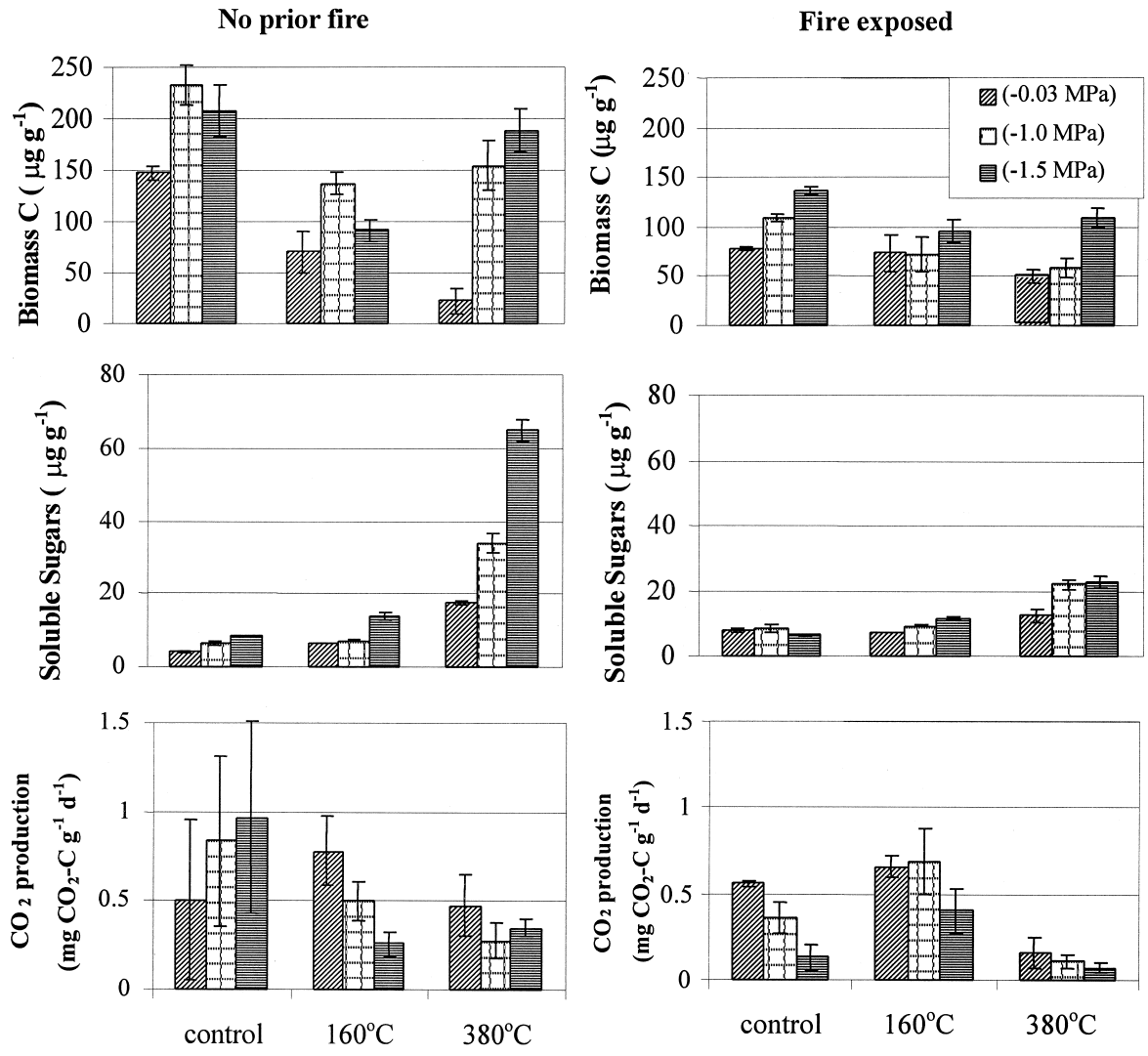

Fig. 3. Soil microbial biomass C, soluble hexose sugars, and basal respiration (CO_2 evolution) at 0.03, 1.0, and 1.5 MPa water potential 14-d after exposure of soils to temperatures of 25, 160, or 380°C (error bars indicate ±1SE).

formation and microbial adaptation to stress in dry-soils during the pre-treatment incubation period. The ability to slow down metabolism by becoming dormant or producing spores may have given microbes a better chance to survive stress from heat exposure or become primary soil colonizers after a fire (Dunn et al., 1985).

Temperatures selected for this experiment were in excess of 120°C, therefore, microbial mortality was perhaps one of the more important contributors to the increased pool of soluble sugars observed following heating. This line of reasoning is supported by Diaz-Ravina et al. (1992) who reported that 70% of mineralized C following heating originated from dead microbial tissues. Additionally, Fernandez et al. (1997) found that temperatures around 350°C resulted in 90% destruction of non-microbial tissue related, water-soluble polymeric sugars, such as cellulose and hemicellulose, to hexose monomers, dissaccharides and glycosides.

Immediate increases in labile soil N (PMN) concentrations at 160°C can be attributed to the release of simple organic compounds from heat-disrupted soil organic matter and heat-killed microbial tissues (see Pietikainen and Fritze (1993)). However, temperatures of 160°C resulted in only a modest increase in PMN concentrations in the soil not exposed to fire compared to a marked increase in the soil previously exposed to fire. Our observed differences in the release of PMN from the two soils perhaps resulted from the presence of structurally different forms of labile N initially present in the two soils (Pietikainen et al., 2000). Furthermore, distillation of organic matter is initiated between temperatures of 200 and 315°C (DeBano, 1990), however, combustion of organic matter at exceedingly high temperatures can result in complete oxidation followed by potential volatilization of N previously held in complex forms (Giovannini et al., 1990). This is supported by the more rapid rate of net mineralization demonstrated by the large NH_4^+–N concentrations in these soils. Similar changes in NH_4^+–N concentrations were observed by Kovacic et al.

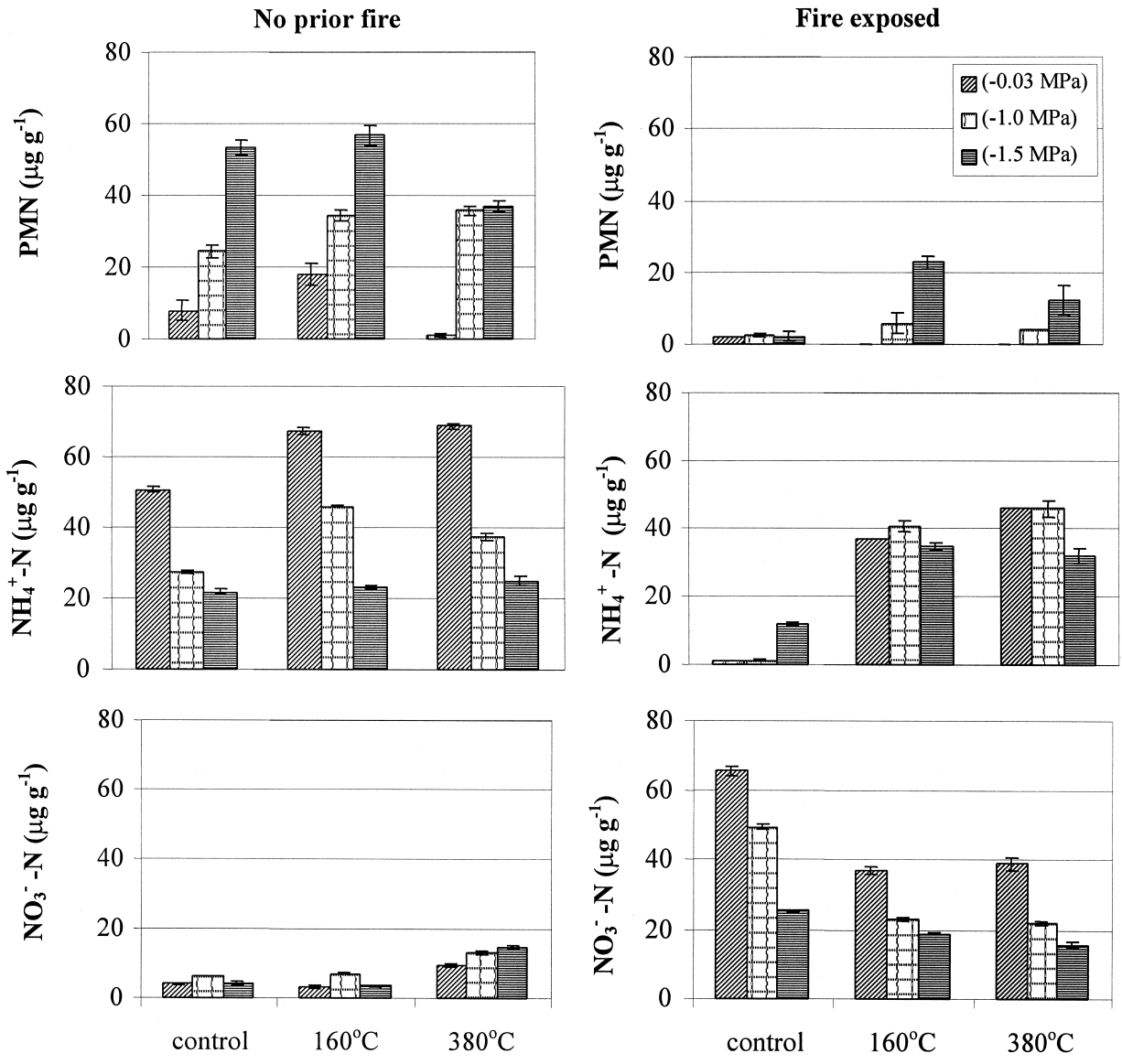

Fig. 4. Potentially mineralizable N, NH_4^+–N, and NO_3^-–N, at 0.03, 1.0, and 1.5 MPa water potential 14-d after exposure of soils to temperatures of 25, 160, or 380° C (error bars indicate ± 1SE).

(1986), Ryan and Covington (1986), and Hernandez et al. (1997) which were attributed to the pyrolysis of compounds derived from live and dead organic matter present in the soil. In research by Dunn et al. (1985), the concentration of inorganic N was positively correlated with burning intensity and initial soil organic matter content.

The lack of change in NO_3^-–N concentration immediately following treatment was a result of insufficient heat to initiate volatilization of NO_3^-. Temperatures must exceed 400°C to result in heat-induced NO_3^- volatilization (Bossatta and Ågren, 1995) which is in excess of the highest temperature used in this experiment.

4.2. Treatment effects 14-d after heating

The unheated control soils had microbial biomass C and soluble sugar levels similar to those prior to incubation which were likely controlled by the limited supply of available C and rapid turnover of the microbial biomass (Bauhus et al., 1993). The observed increase in soluble sugars following heating is supported by earlier findings which showed that drying and re-wetting of soils result in a release of soluble sugars followed by a gradual return to background or near background levels (DeLuca, 1998).

The release of available C and N upon heating supported recovery of microbial activity even under conditions of low water potential. A significant drop in the concentration of soluble ARC in both soils over time resulted from possible microbial consumption of hexose sugars released upon heating. However, drier soils had greater levels of soluble ARC accumulation perhaps as a result of slowed C mineralization and consumption rates. Stressed conditions in the moist soils

upon heating were further demonstrated by the high rates of respiration in moist, heat-treated soils. These differences in respiration likely resulted from differences in both, microbial community structure and the availability of substrate (Pietikainen et al., 2000).

The observed changes in soil N pools following heating are similar to our findings from field studies (DeLuca and Zouhar, 2000; Choromanska and DeLuca, 2001) in which fire initially resulted in a release of mineral and labile N followed by a significant reduction in PMN within one year following fire. This loss of PMN is observed in comparison of the unheated control soils of the fire exposed versus the soils not exposed to fire. The fire exposed soil had low levels of PMN which were likely depleted by heat induced volatilization and subsequent mineralization of labile N. Additionally, field studies have shown that fires of lower severity and thus lower heat penetration into mineral soil result in significantly lower losses of labile N compared to high severity fires (Choromanska and DeLuca, 2001).

Soil water potential had a significant effect on the process of N mineralization post-heating where soils with the highest soil water potential had the greatest decline in PMN followed by the greatest accumulation of net inorganic N (Pulleman and Tietema, 1999). A positive correlation between soil moisture content and the NO_3^-–N in the fire exposed soil suggested that recovery of nitrifying organisms were more directly influenced by available moisture than by NH_4^+–N availability.

Previous site management and disturbance history must be considered to effectively predict the potential influence of fire on soil nutrient concentrations. The two soils used in this experiment differed significantly in their biochemical composition due to previous exposure of one soil to fire. Prior exposure of soils to wildfire resulted in low initial levels of microbial biomass, yet rapid rates of N mineralization. This was reflected by the low concentrations of biomass C, PMN, soluble sugars, and NH_4^+–N in the soil exposed to wildfire. When the soils were collected for the purpose of this experiment, the population of nitrifiers in the fire-exposed soil apparently had partially recovered and increased the levels of soil NO_3^-–N. In contrast, the soil not exposed to fire had relatively high levels of microbial activity and low concentrations of NO_3^-–N until the end of the study.

Low soil water potential may protect newly formed labile N reserves that remain longer in drier soils than in more moist soils regardless of soil fire history. Such dry soil conditions occur in the field during summer wildfires and fall prescribed fires as opposed to the moist soil conditions often associated with spring prescribed fire.

It is important to recognize that the temperatures used in this experiment are in excess of temperatures commonly found at depth in mineral soils. As indicated above, heat transfer into mineral soil during fire events is limited by the insulating effect of the porous soil medium and the latent heat of vaporization associated with soil moisture. This limited heat transfer requires that the above results be extrapolated with care. It is unlikely that the temperatures used in this experiment would be reproduced in natural mineral soils below a depth of 3 cm with the exception of heating under large woody fuels and during the burning of forest harvest residuals. Nevertheless, the results clearly demonstrate the important role of soil moisture and prior fire history on the effect of fire on soil biochemical properties.

Acknowledgements

The authors wish to thank Caitlin Morse and Kris Zouhar for lab assistance and Jay Norton and Cathy Zabinsky for review of this manuscript. This project was partially supported by funding from NSF and the USFS Rocky Mountain Research Station.

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